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Adaptive Management for Threatened and Endangered Species***

Articles

An Adaptive Decision Framework for the Conservation of a Threatened Plant

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Abstract

Mead's milkweed *Asclepias meadii*, a long-lived perennial herb of tallgrass prairie and glade communities of the central United States, is a species designated as threatened under the U.S. Endangered Species Act. Challenges to its successful management include the facts that much about its life history is unknown, its age at reproductive maturity is very advanced, certain life stages are practically unobservable, its productivity is responsive to unpredictable environmental events, and most of the known populations occur on private lands unprotected by any legal conservation instrument. One critical source of biological uncertainty is the degree to which fire promotes growth and reproductive response in the plant. To aid in its management, we developed a prototype population-level state-dependent decision-making framework that explicitly accounts for this uncertainty and for uncertainties related to stochastic environmental effects and vital rates. To parameterize the decision model, we used estimates found in the literature, and we analyzed data from a long-term monitoring program where fates of individual plants were observed through time. We demonstrate that different optimal courses of action are followed according to how one believes that fire influences reproductive response, and we show that the action taken for certain population states is informative for resolving uncertainty about competing beliefs regarding the effect of fire. We advocate the use of a model-predictive approach for the management of rare populations, particularly when management uncertainty is profound. Over time, an adaptive management approach should reduce uncertainty and improve management performance as predictions of management outcome generated under competing models are continually informed and updated by monitoring data.

Keywords: adaptive management; *Asclepias meadii*; Mead's milkweed; population dynamics; population viability; threatened and endangered species; uncertainty



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Introduction

Conservation of threatened and endangered species (TES) of plants is a decision problem regarding the selection of management actions that result in a high probability of population persistence. Prescriptive actions might include manipulation of habitats, populations (i.e., transplanting, reintroduction), or regulations of human activity. Management decisions must be evaluated according to how the target population responds and whether progress toward conservation goals is achieved. However, conservation outcomes can be difficult to predict accurately because of uncertainties about how the system functions, about the unpredictable environment, and about the degree to which control can be exerted over the system. Furthermore, conservation outcomes can be difficult to measure accurately because TES populations usually cannot be observed completely.

Because the future condition of a population of a TES is a consequence of its current condition and all intervening management actions and stochastic events, it follows that a good conservation decision today should take into account the future course of decision making, as well as future uncontrollable events (Clark and Mangel 2000; Runge 2011). Thus, a management decision, the focal plant population, and its random environment constitute a stochastic dynamic system, and finding a good conservation strategy for TES is an optimal control problem (Williams 1989). Further, a dynamic approach to TES conservation provides the setting for applying an adaptive framework to account explicitly for ecological or structural uncertainty, which we define as the uncertainty regarding the average response of the system to management. Adaptive resource management is an iterative decision-making process that seeks an optimal management policy (i.e., a condition-dependent prescription for action) in the face of structural uncertainty, and it uses feedback from the resulting decisions to reduce the uncertainty for future decisions (Walters 1986; Williams et al. 2009). Uncertainty is characterized by a set of competing, plausible representations of the system, or decision models, and the decision policy evolves in response to a continuous stream of information on the relative predictive performance of those models (Moore et al. 2011).

An adaptive decision-analytic approach departs significantly from a popularly used alternative, population viability analysis (PVA; Morris and Doak 2002). Population viability analysis has received widespread use in assessing the likelihood of persistence of plant species (Fiedler 1987; Menges 2000; Bell et al. 2003) and sometimes to identify management regimes. However, the PVA approach has two important shortcomings that limit its usefulness for managing TES in the face of uncertainty. The first is its inability to account for the serial dependency of conservation actions. Because a PVA does not dynamically link management decisions to conservation goals and a changing population state, decisions identified by a PVA are not population-state-dependent (Westphal et al. 2003). Second, while the PVA approach typically accounts for stochastic uncertainty, often via simulation, structural uncertainty is not usually formally accommodated (Pascual et al. 1997). In general, the PVA approach provides no guidance for management under structural uncertainty and offers no formal means to incorporate learning into management (Moore et al. 2010). Therefore, we believe that a PVA provides an incomplete framework for making decisions in the context of managing a rare and poorly understood dynamic resource.

Our objective was to demonstrate a formal, decision-analytic application of adaptive resource management to the recovery of a threatened plant, Mead's milkweed *Asclepias meadii*. We propose a framework for deriving management policies that recognizes that decisions about the plant will always be made using incomplete information. At the same time, the framework systematically reduces uncertainty by using feedback from monitoring, resulting in more informed subsequent decisions.

Biology and conservation status of Mead's milkweed

Mead's milkweed is a perennial, dicotyledonous prairie herb, one of approximately 165 species of the milkweed family Asclepiadaceae (USDA 2008). Endemic to mesic tallgrass prairie and glade communities within the central United States, the species has experienced population declines and local extirpations throughout its range, leading to its 1988 designation as threatened



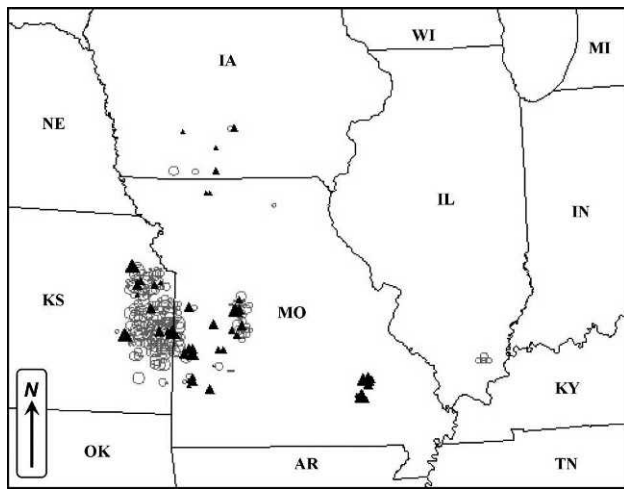


Figure 1. Distribution of 275 extant, naturally established populations of Mead's milkweed *Asclepias meadii* in the United States. Populations occur on sites either with (▲) or lacking (○) a specific conservation focus. Size of symbol is approximately proportional to population size at most recent survey (1951–2008; median survey year = 1995). Locations are spatially accurate only to county level. Populations have been artificially reintroduced (not shown) in former parts of the historic range, including northwestern Indiana (2), northern Illinois (5), and southwestern Wisconsin (7).

by the U.S. Fish and Wildlife Service (USFWS 1988) under the U.S. Endangered Species Act as amended (1973; 16 U.S.C. 1531–1543). Mead's milkweed is vulnerable to the alteration or destruction of habitat from agriculture, urbanization, and recreation, which have occurred in this region since European settlement. Such changes may have disrupted adaptive processes critical to the plant's reproductive biology, making it particularly vulnerable to extinction.

The historic range of Mead's milkweed extended from Kansas through Missouri and Illinois to southern Iowa, southwest Wisconsin and northeast Indiana (Figure 1). Mead's milkweed persists in ≥ 275 sites ("populations") in four states (USFWS 2003; K.J. Lah, USFWS, unpublished data). Ninety-three percent of known populations are clustered in eastern Kansas and western Missouri, with the remainder on isolated sites in southern Iowa, southeastern Missouri, and southern Illinois. Populations were extirpated from Wisconsin and Indiana, and reintroduced populations are monitored in those states.

Mead's milkweed is a long-lived plant that reproduces both vegetatively, through the spread of root stock or rhizomes, and sexually. An individual may produce numerous vegetative clones, but sexual reproduction is thought to be crucial for maintaining high genetic diversity, providing some insurance of long-term population maintenance in general and protection against chance extirpation in particular (Tecic et al. 1998). Viable seed is only produced by outbreeding in most milkweeds, because they are either sexually self-incompatible or highly sensitive to inbreeding depression (Kephart 1981; Shannon and Wyatt 1986; Kahn and Morse 1991; Sage and Williams 1991; Broyles and Wyatt 1993).

Pollination by miner bees *Anthophora* spp. and bumblebees *Bombus* spp. occurs in late spring during a short flowering period, with fruit appearing by late June (Betz 1989; Betz and Lamp 1992; Betz et al. 1994). Seed pods mature by mid-October (Morgan 1980; *Supplemental Material*, Reference S1; <http://dx.doi.org/10.3996/012011-JFWM-007.S1>; Kurz and Bowles 1981; *Supplemental Material*, Reference S2; <http://dx.doi.org/10.3996/012011-JFWM-007.S2>). Individuals planted as 1-y-old juveniles in field experiments flowered in as few as 2 y, but plants grown from seed at the same sites were projected to take ≥ 15 y to reach reproductive size (Bowles et al. 2001; Hayworth et al. 2001). In any year, a mature plant may produce one or more flowering stems and multiple nonflowering stems, nonflowering stems only, or may recede to a tuber stage. Mead's milkweed persists in fire-adapted communities and increases seed production in response to burning (Bowles et al. 1998). Because of its multiple reproductive strategies, sites comprised of many adult stems may represent a population of individual genotypes or a few genetic individuals with extensive clonal spread.

The primary recovery strategy of the USFWS for Mead's milkweed is to reduce the threats that have led to the listing of the plant by working with interested landowners on management actions beneficial to the plant's habitat (USFWS 2003). Only 2.9% of known Mead's milkweed populations occur on federal lands where the species is protected under the Endangered Species Act. Another 15.6% of sites occur on lands with varying degree of conservation status and legal protection, including state lands, private and county conservation lands, and private lands under formal or informal conservation agreements. The vast majority (81%) of sites occur on private lands under no conservation status whatsoever, which are mostly managed for agricultural and commercial purposes (USFWS 2003, appendix 2; updated 2008; K. J. Lah, unpublished data).

Factors driving the decline of Mead's milkweed may include (in no particular order) the conversion of suitable habitat, reduced populations of specialized pollinators, herbivory, introduction of competitors, succession to woody cover induced by exclusion of fire, habitat fragmentation, and detrimental management practices on suitable habitats (Betz 1989; USFWS 2003). The primary income-generating use on lands occupied by Mead's milkweed is hay production, while other uses such as grazing are far less prevalent (USFWS 2003). Typically, spring and summer mowing takes place on privately managed lands. Annual mowing virtually halts sexual reproduction in Mead's milkweed by removing the seeds before they mature (Freeman 2006), and some evidence suggests that mowing promotes vegetative growth over reproductive development (Bowles et al. 1998; Tecic et al. 1998).

A variety of approaches has been proposed to restore populations of Mead's milkweed, including cessation or rescheduling of mowing, implementation of prescribed burning, augmentation or reintroduction of seed or plants, chemical or mechanical control of invasive plants and woody stems, hand-pollination, promotion of key

pollinator species, and introduction of soil disturbance to facilitate germination (USFWS 2003). Specifically, summer mowing in alternate years, with either autumn mowing or no mowing during the intervening year, allows for some reproductive activity. To many landowners though, such forms of economic sacrifice—even for favorable conservation outcomes—are unacceptable.

Prescribed burning is applied to private and public lands during the dormant season. Burning is believed to increase flowering and seed production, stimulate dormant root stock, increase seedling and juvenile survival, and increase genotypic diversity of Mead's milkweed (Bowles et al. 1998; Tecic et al. 1998). The effects are thought to be enhanced in wet years, but do not appear in years following mowing (Kettle et al. 2000; Grman and Alexander 2005). Prescribed fire is also used to maintain the species' habitat and control invasive species and woody plants. Augmentation or reintroduction, through the manual planting of seeds and year-old root stock, is used to increase the number of populations. Faster growth and increased survival appear to be associated with artificially propagated plants and seeds when combined with burning and above-average precipitation (Bowles et al. 1998; Bowles et al. 2001). Augmentation or reintroduction efforts have been attempted at some sites, and this work is ongoing (Bowles et al. 1998; Bowles et al. 2001; USFWS 2003). Sites heavily impacted by invasive or woody species may require an integrated approach of herbicide, mechanical removal, and/or prescribed fire.

Since the plant's 1988 listing, some recovery actions have been taken, new populations have been discovered, and some populations have been lost. By 2008 the plant's status was essentially the same as when it was listed and not significantly closer to achieving the recovery criterion of 21 "highly viable" populations within its historic range (USFWS 2003).

Methods

We conducted our work in a series of TES-focused workshops held as part of an Adaptive Management Conference Series. Our investigative team broadly consisted of scientists who work with Mead's milkweed and know the biology well, along with individuals with expertise in modeling population dynamics or adaptive management frameworks. We initially approached this problem systematically and tried to move through the process carefully. However, the group quickly got trapped in biological detail without having a clear overview of what we were trying to achieve. This triggered our decision to move to a rapid prototyping approach (Nicolson et al. 2002). At this stage, we had already constructed a provisional matrix population model, and used it to develop our overview. Given this, we worked through the adaptive-management development process more coherently, by focusing on the following five questions:

1. What is the objective of management?
2. What is the management decision?

3. What uncertainty impedes the decision of the manager?
4. How does monitoring feed back to update the system?
5. What is the state-dependent optimal policy?

We worked through these questions in the following sections, first diagnosing what makes decision making difficult, then expressing an objective for management, selecting a menu of management alternatives, developing predictive models, and finally introducing optimization tools for computation of adaptive decision policies (Runge 2011).

Impediments to decision making

Several profound uncertainties obscure the choice of appropriate management actions for Mead's milkweed. First, key phases of the plant's life cycle are poorly understood. Several population parameter estimates (e.g., germination rate, individual growth rate) are based on greenhouse experiments rather than in situ populations (Betz 1989). Managers are highly uncertain about key mechanisms that limit reproduction and survival and which forms of management best target these mechanisms (Bell et al. 2003). Second, the plant's long period of immaturity, its unpredictable transition among different flowering and vegetative stages, and its low rate of recruitment make short-term assessment of management actions difficult (Bowles et al. 2001). Learning about the efficacy of any approach is likely to occur very slowly and only with sufficient replication. Third, even with an intense monitoring effort, populations are only partially observable, so an unbiased assessment of the population stage structure at any time is practically impossible. The plant's flower is inconspicuous, and detecting a flowering adult stem can be difficult in all cases except where intensive surveys are feasible (for example, in small, defined patches of a few hectares [Kettle et al. 2000; Alexander et al. 2009]). Detection of juvenile or nonflowering adult stages is not reliable with current field methods at any practical scale (Alexander et al. 1997), and many plants apparently remain undetected in their dormant underground stage. Furthermore, only laboratory analysis can confirm whether two stems represent genetically distinct individuals (Tecic et al. 1998). In the field, genetic individuality can be roughly inferred by the spacing between stems, but clonal spread (and thus, spacing) is often a function of management treatment (Bowles et al. 1995; *Supplemental Material*, Reference S3; <http://dx.doi.org/10.3996/012011-JFWM-007.S3>; Alexander et al. 1997; USFWS 2003). Because decisions are based on a population's apparent rather than true state, management can be counterproductive if the effectiveness of the action depends on the true, but unknown, status of the population (Moore and Kendall 2004).

Perhaps the most fundamental impediment to effective conservation of Mead's milkweed is bureaucratic. Because the plant is dispersed across lands having different owners, including public and private, there is no single decision-making authority. Different owners bring a range of land management objectives and varying degrees of mandate for plant recovery. Thus, implementing a



comprehensive recovery program for the species requires a great deal of cooperation and coordination. There is potential through the Mead's milkweed recovery plan (USFWS 2003) to provide a mechanism for achieving large-scale recovery. For this work, we elected to focus only on those populations where we could control management actions and could periodically monitor the population. Thus, the scale of our decision framework is at the level of an individual population, which we define as one or more individual plants occurring in a contiguous patch of habitat. To provide context for this definition, the recovery plan provides highest viability ranking to sites comprising ≥ 50 adult plants occurring in patches of ≥ 50 ha of available late-successional stage habitat (USFWS 2003).

Objective for decision making

The fundamental management objective for the global Mead's milkweed population is to maintain its persistence over a prolonged period. The primary delisting criterion in the Mead's milkweed recovery plan is to maintain 21 highly viable populations distributed across different tallgrass prairie and glade communities and 11 physiographic regions (USFWS 2003). At the scale of a single habitat patch, a reasonable goal may be to maximize the population (or its adult component) in the context of a very long time frame. This serves only as a "means objective" to the fundamental objective of species-wide persistence, but a key one, we believe, because any management strategy that achieves a large, enduring population has, by definition, achieved a "highly viable" population.

From a practical standpoint, an optimal management policy also involves the minimization of management costs. Because time and resources are always limited, beneficial treatments cannot always be applied frequently, so we wish to identify a solution that uses as few resources as possible to achieve the recovery objective. Thus, we express the management goal in terms of increasing population size, but subject to a cost penalty whenever an action is implemented. With an appropriate cost assigned to each action (see Optimization section below), the optimization should seek to increase population size and avoid local extirpation, but not unnecessarily spend limited resources to do so.

Management actions

The most acute biological challenges in managing for population growth, and ultimately persistence, of Mead's milkweed are poor rates of sexual reproduction and slow growth to maturity (Bowles et al. 2001). Our group considered several factors resulting in low production of fruit, including incompatible management, high levels of herbivory, nutrient shortage, insufficient pollination, and rainfall extremes. Of these, rainfall is outside the control of managers, and pollination can only be enhanced by labor-intensive and inefficient hand-pollination. Though it may be possible to reduce herbivory and increase the number of fruits surviving to maturity by excluding or otherwise deterring predators (Grman and Alexander 2005), large-scale exclusions are impractical. Cessation of hay mowing would likely free reproductive limitations,

but areas that would be most affected by mowing are under private ownership, and not subject to management by conservation authorities. Perhaps the most potent manipulation to boost fruit production and accelerate rates of establishment and growth to maturity is controlled burning. It is thought that fire releases nutrients stored in fuels, which relaxes the nutrient limitations to reproduction (Grman and Alexander 2005), or that the consumption of dead litter removes a light limitation (Hulbert 1988); in either case, the effect appears to be enhanced when there is high rainfall during the preceding year (Kettle et al. 2000; Grman and Alexander 2005).

Based on our limited knowledge of the effects of actions potentially available to conservation authorities, we selected burning as the decision instrument for the management of Mead's milkweed populations. We considered cessation of mowing as a precondition for managed populations, because we wish to guarantee their ability to set seed. Specifically, the recurring management decision is whether or not to carry out burning during the current year, a decision that is triggered by current population status.

Predictive models

Based on published parameter estimates, our own estimates from a long-term mark-recapture study, and basic life-history information, we constructed a matrix population model for Mead's milkweed, following Caswell (2001; also see Bell et al. 2003; Bell and Bowles 2006). This model projected growth of a population through time in response to annual decisions about fire and unpredictable stochastic effects. We considered four discrete life-history stages during the flowering period each year (Figure 2): juveniles or seedlings (*J*); a below-ground "tuber" stage (*T*; either dormant tubers, or adult stems lost to herbivory); plants with only nonflowering adult stems (*N*); and plants with flowering adult stems (*F*). Because ramets (stems) may be from the same genet (genetic individual) and these subterranean links are unobservable, we followed Alexander et al. (1997) and used patches of stems as an approximate population metric. "Patches" of Mead's milkweed were groups of stems separated by >1.25 m from any other stem and were either "flowering" (at least one flowering stem within the group) or "nonflowering" (all stems within the group lacking flowers). The transition matrix contains the annual probabilities of transitions among stages (ψ^{UV}) and production of juveniles ($f \times \gamma = \text{seed production} \times \text{germination}$) in the following spring:

$$\begin{bmatrix} n_J \\ n_T \\ n_N \\ n_F \end{bmatrix}_{t+1} = \begin{bmatrix} \psi^{JJ} & 0 & 0 & f \times \gamma \\ 0 & \psi^{TT} & \psi^{NT} & \psi^{FT} \\ \psi^{JN} & \psi^{TN} & \psi^{NN} & \psi^{FN} \\ 0 & \psi^{TF} & \psi^{NF} & \psi^{FF} \end{bmatrix} \begin{bmatrix} n_J \\ n_T \\ n_N \\ n_F \end{bmatrix}_t$$

The population vector, a list of the number of units in each stage, for the next year $t + 1$, can be obtained as the product of the population projection matrix and the population vector at the current year t . Each element in

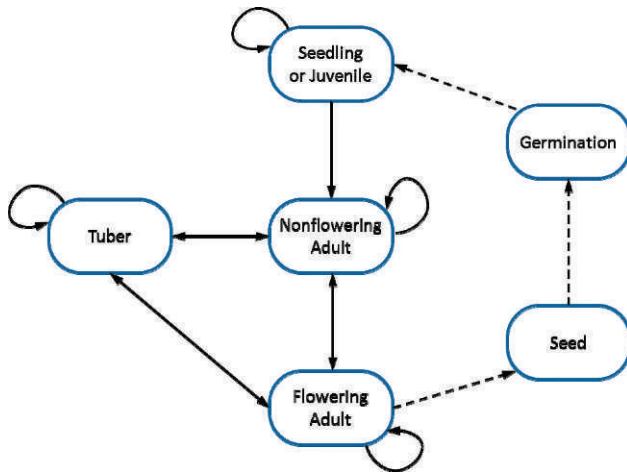


Figure 2. Summary of stage transitions in life-cycle model of Mead's milkweed *Asclepias meadii*. Solid arrows represent annual transitions among the four population stages, and broken arrows represent within-year components of recruitment. Self-referential arrows represent survival of individuals in a particular life stage.

the projection matrix is an annual transition probability in the life cycle, as represented by a solid arrow in Figure 2. For example, ψ^{NF} is the probability that a nonflowering patch in one year survives and becomes a flowering patch 1 y later.

Juvenile parameters. Transitions involving the juvenile stage (i.e., transitions into, within, and out of that stage) are extraordinarily difficult to assess in the field, and so few such studies exist. We interpreted results from literature sources to parameterize these stages of the model.

Bowles et al. (2001) reported an average survival rate of 0.35 (survival to the end of the first growing season) for planted seeds at seven prairie sites. At three of these sites, Bowles et al. (1998) observed greater survivorship and larger individuals in burned sections of the sites than in unburned sections, with effect size of 0.85 (logit scale) being the largest observed. In our model, we specified a 0.35 juvenile survival rate in any year that the site was not burned and 0.56 in any year that it was burned, the difference corresponding to this effect size (Table 1).

Mead's milkweed may persist in a juvenile stage for many years, but the average length of time in this stage and its variance is speculative. Betz (1989) stated that the flowering adult stage was not reached for ≥ 4 y. Bowles et al. (2001) reported that flowering occurs only after the plant reaches a threshold leaf-area index, which (based on growth projections of juvenile plants) they concluded could not be reached for ≥ 15 y. In our model, we allowed the conditional (on survival) transition from the juvenile to the nonflowering adult stage to vary uniformly from 0.067 to 0.10 annually (Table 1), corresponding to a range of 10–15 y as the average time spent in the juvenile stage; this range is consistent with projections demonstrated at the study sites of Bowles et al. (2001).

We modeled the transition into the juvenile stage as the product of adult stem fertility, fecundity, and

germination rates, with each derived from literature sources. Fertility rate of Mead's milkweed is low and highly variable. Betz (1989) estimated that 6.4% (range = 0–14%) of flowering stems produced fruit. On sites in southwest Missouri in 2005, 23% of flowering stems produced fruit (Eulinger and Skinner 2005; *Supplemental Material*, Reference S4; <http://dx.doi.org/10.3996/012011-JFWM-007.S4>). Kettle et al. (2000) found that 14.9% of flowering stems produced mature fruit. They also observed a greater rate of fertility in years in which the site was burned rather than unburned (effect size of 0.91 on logit scale). Although the difference was not significant, the effect appeared to be magnified when rainfall in the previous year was greater than expected. In our model, we allowed fertility rate to vary uniformly between 0.001 and 0.23, reflecting stochastic uncertainty in its annual value and the potential occurrence of multiple flowering stems in a single patch. We reasoned that application of fire would increase the limits of this range, therefore, the limits under burning were 0.002–0.43, reflecting incorporation of the logit-scale effect size of 0.91 (Table 1).

Average fecundity is consistently reported around 60 seeds per pod (Betz 1989; Betz and Lamp 1992; Bowles et al. 1998; Row et al. 1999), with no evidence of fire-related differences. In our model, we used the range provided by Betz (1989) and permitted fecundity to vary uniformly between 55 and 68 seeds per pod on both burned and unburned sites (Table 1).

Limited published data on germination of Mead's milkweed exist outside of greenhouse studies. Betz (1989) reported a germination rate range of 0.385–0.506 over 7 y of cultivation of 2,429 seeds. Whether germination rate is enhanced following fire is unknown; in our model, we took the lower limit of the range (0.385) as our value of germination rate for either the burned or unburned treatment (Table 1).

Adult parameters. We estimated transitions among the below-ground, nonflowering adult, and flowering adult stages from data obtained from a long-term mark-recapture study of a population of Mead's milkweed on Rockefeller Native Prairie in northeastern Kansas. A complete description of study design and field methods is found in Alexander et al. (2009). Patches (as defined above) of Mead's milkweed were searched for, classified as flowering or nonflowering, and uniquely marked in a systematic survey conducted annually in late May or early June from 1992 to 2006. In even-numbered years of the study, the prairie was burned in April prior to the emergence of stems. Following a revision of the site's management plan, the prairie was also burned and surveyed in 2007. However, the survey that year was performed twice by independent teams of observers in order to obtain a direct estimate of detection probability of patches given the known presence of stems.

Our interest was in representing transition rates among dormant, nonflowering, and flowering stages as a function of a decision variable under management control (prescribed burning) and an uncontrolled stochastic environmental variable (rainfall). Therefore, we fit a series of multinomial models to 252 patch capture

Table 1. Ranges of parameters for juvenile stages of the life-cycle model for Mead's milkweed *Asclepias meadii*. For some parameters, ranges differ according to whether burning is applied or not. For two parameters, alternative ranges for the burning option are entertained under a competing model. To reflect temporal stochasticity in parameters, a uniform distribution was used for sampling parameters during optimization. Where the range is represented by a single number, the parameter was assumed deterministic.

Transition group ^a and parameter	Parameter range	
	No burning	Burning
Transitions into juvenile stage (ψ^{FJ})		
Fertility rate (proportion flowering stems with pods)	0.001–0.230	0.002–0.430
Fecundity (seeds/pod)	55–68	55–68
Germination rate		
Model 0: "Baseline"	0.385	0.385
Model 1: "Burn-enhanced"	0.385	0.506
Transition within juvenile stage (ψ^{JJ})		
Annual survival	0.350	0.560
Transitions out of juvenile stage (ψ^{JN})		
Conditional annual transition probability		
Model 0: "Baseline"	0.067–0.100	0.067–0.100
Model 1: "Burn-enhanced"	0.067–0.100	0.250–0.333

^a Notation: ψ^{ij} denotes an unconditional transition probability from stage i to stage j (J : juvenile, N : nonflowering, F : flowering).

histories over 1992–2006, which included covariates for the presence or absence of burning (B) in the current year and the amount of rainfall (percent deviation from long-term average; Kettle et al. 2000) in the prior year (r). Transition rate was decomposed into a year- and stage-specific survival component, S_i^u , and a conditional (on survival) transition probability, $\phi_i^{uv}(B, r)$. The product of the two parameters provided the unconditional transition probability used in our matrix projection model:

$$\psi_i^{uv}(B, r) = S_i^u \phi_i^{uv}(B, r).$$

We used Program MARK (White and Burnham 1999) to fit the models and obtain parameter estimates for our transition model.

Details on model-fitting procedures and estimation results are provided elsewhere (*Supplemental Material*, Text S1; <http://dx.doi.org/10.3996/012011-JFWM-007.S5>), but we mention here certain assumptions we made in order to obtain estimates in the face of sparse data. First, we assumed perfect detection of patches with flowering stems (i.e., probability of encountering a flowering patch given its occurrence = 1.0) and constant detection rate of nonflowering patches. For a cryptic plant such as Mead's milkweed, even in its flowering stage, detection of flowering stems is imperfect. This is certainly the case for first-ever detection of a flowering patch (0.40–0.62; Alexander et al. 2009); however, detection of a previously detected flowering patch is substantially greater (approx. 0.90; H.M. Alexander, University of Kansas, unpublished data), thus, the assumption may not be unreasonable for purposes of application at a habitat patch scale where focused monitoring can be conducted. Detecting nonflowering patches may be somewhat more likely following a burn (Alexander et al. 2009), but the plant in this stage is uniformly difficult to detect under any

condition, so assuming a constant detection rate of nonflowering patches is a reasonable simplifying assumption. Second, we assumed that transition out of the dormant stage to either the nonflowering or flowering stages was impossible (probability = 0) in any year that a burn was not conducted. Again, this is a simplification, but the consensus of the literature suggests that the transition rate is low, so the assumption may be reasonable. Third, while we permitted rates of transition among stages to vary through time in response to management and rainfall, we assumed that stage-specific rates of survival were constant over the period of study (Alexander et al. 2009). This assumption seems consistent with the emphasis of most long-term studies that explain the appearance and disappearance of stems more as a function of environmental-driven transition into and out of the dormant stage than as a function of time-varying survival.

Addressing structural uncertainty through alternative model parameterizations. The full set of transition parameters for the juvenile and nonjuvenile stages completely specifies our matrix population model (Figure 2). However, each parameter is accompanied by uncertainty, which, in some cases, is considerable. We believe that the parameter estimates incorporate the best information across the range of available literature on the species. Even so, we could not sufficiently quantify portions of the life cycle, owing to the lack of available estimates. Incorporating parametric uncertainty in decision models requires additional model structure to represent plausible values for each uncertain parameter, but the methods available for deriving an optimal decision policy (see below) are acutely limited by problem dimensionality (i.e., the number of population states, candidate actions, and stochastic variables).

In light of this, we focused attention on parts of the model involving the juvenile stage. This stage has proven the most difficult to observe and experimentally manipulate in field settings (Betz 1989; Bowles et al. 1998), and many of the important parameters in this stage are speculative and based on incomplete or anecdotal information. Burning of Mead's milkweed sites is considered to be a positive management strategy with a net effect of boosting population growth (Betz 1989; Bowles et al. 2001). However, the degree to which growth is enhanced is unclear. Therefore, we considered two competing hypotheses about the effect of burning on key parameters in the juvenile stage. Our model described above (Model 0) characterized a "baseline" scenario, in which burning increases fertility rate and juvenile survival (Table 1), as is conventionally thought, but does not affect other components of recruitment. A "burn-enhanced" scenario (Model 1) employed the same model structure as the first, but expanded the effects of burning on juvenile stage transitions (Table 1). First, the rate of germination is assumed to increase under burning, from the baseline rate of 0.385 to 0.506, the greatest average rate observed by Betz (1989). Second, probability of transitioning out of the juvenile stage increases under burning from the range of 0.067–0.10 to a range of 0.25–0.33, implying a shorter time of 3–4 y until first reproduction, based on garden experiments (Bowles et al. 1998).

Using deterministic point estimates for the matrix elements, both models produced an asymptotic growth rate of $\lambda = 0.9$ when no burning takes place, projecting a population decline to extirpation. When burning is applied, asymptotic growth rate increased to 1.1 under Model 0 and to 1.3 under Model 1, reflecting model-specific differences in the influence of burning on milkweed life history parameters. Clearly, conditional on the model set and associated parameter estimates, the simplest conclusion is that burning all the time is the optimal management strategy. However, as discussed earlier, less intensive management might achieve the same population persistence goal. Hence, we took into account costs of burning in optimization.

Optimization

Given the available information regarding population dynamics of Mead's milkweed, we sought an optimal decision policy for its management where optimal decisions could be indexed to distinct population states. To obtain such a solution, it is natural to express the problem as a Markov decision process (Bellman 1957). Five components comprise a Markov decision process: a set of system states (e.g., specific combinations of the four population stages), a set of candidate actions, a model of system dynamics for the movement of the system among states in response to a series of annual actions, a reward function that returns the value of making a particular decision in the current state, and a discount rate that establishes the value of a reward earned in the future relative to its value today. Given these elements, the recursive optimality equation of Bellman (1957) is used to compute an optimal time and

state-dependent decision policy to maximize the discounted sum of rewards (Williams et al. 2002; Moore and Conroy 2006). The policy provides an optimal decision at the current time step, followed by a sequence of optimal future decisions, conditional on the current decision and population state.

Our reward function was the discounted and cost-weighted sum of number of flowering patches over an arbitrarily long time horizon, and our objective was to maximize this value through the application of burning over time. The annual reward is simply the number of flowering patches produced. However, in any year that a burn is used, the reward is valued at 0, which is a simple way of factoring in cost. Finally, we discounted each reward by the discount rate 0.986. This rate is slight from a conservation perspective (i.e., a return 50 y from today is half as valuable as realizing it today), but it is sufficient to enable convergence of the optimization algorithm on a stable decision policy.

We calculated the optimal decision policy for this problem using stochastic dynamic programming (Bellman 1957) implemented in Program ASDP (Lubow 1995, 1997). Dynamic programming is a reverse-iterative dynamic optimization procedure that is well-suited for small, discrete problems and optionally allows for the incorporation of stochasticity (see Clark and Mangel 2000). Dynamic programming yields a state-specific strategy that prescribes whether or not to burn during any given year according to the number of individuals in each of the four life-history stages. The stochastic form of dynamic programming allows for the calculation of an optimal policy for system dynamics that are subject to stochastic variation. However, a dynamic programming problem quickly becomes computationally intractable as the number of stochastic variables increases (Williams et al. 2002). To work within these computational constraints, we focused on annual stochasticity in the transition probabilities for juvenile stages (Table 1), and assumed fixed values for below-ground and adult stage parameters (Table 2).

To simplify the optimization problem, we discretized the numbers of individuals in each stage into classes. For juveniles, we selected five classes, at equal intervals from 0 to 400+. For nonjuveniles, we chose five classes, at equal intervals from 0 to 20+. If model predictions resulted in numbers greater than the maximum allowed (400 or 20), those individuals were merged into the last group. Random distributions were used to describe annual variability in rainfall (percent of long-term average; Gaussian, mean = 108%, SD = 23%) and annual variability in rates of juvenile to nonflowering adult transition, fertility, and fecundity (all uniform; Table 1). For each model, we ran the ASDP procedure until a stationary policy was achieved (i.e., decisions were not dependent on time), which we assumed to occur when the set of optimal decisions did not change over 100 successive time steps.

Adaptation

The feature that distinguishes adaptive management from other structured decision-making processes is the



Table 2. Transition probabilities among the nonjuvenile stages in the life-cycle model for Mead's milkweed *Asclepias meadii* estimated from marked individuals followed 1992–2006 at Rockefeller Prairie, Kansas. Probabilities differ according to whether burning is applied (B) or not (NB) and precipitation conditions in the previous year.

Transition group and parameter ^a	Rainfall ^b					
	Below normal		Normal		Above normal	
	NB	B	NB	B	NB	B
From tuber						
To tuber (ψ^{TT})	0.90	0.31	0.90	0.31	0.90	0.31
To nonflower (ψ^{TN})	0	0.54	0	0.54	0	0.54
To flower (ψ^{TF})	0	0.05	0	0.05	0	0.05
Mortality	0.10	0.10	0.10	0.10	0.10	0.10
From nonflower						
To tuber (ψ^{NT})	0.06	0.35	0.18	0.08	0.39	0.01
To nonflower (ψ^{NN})	0.73	0.49	0.68	0.57	0.52	0.44
To flower (ψ^{NF})	0.18	0.13	0.11	0.32	0.06	0.52
Mortality	0.03	0.03	0.03	0.03	0.03	0.03
From flower						
To tuber (ψ^{FT})	0.04	0.01	0.08	0.02	0.12	0.02
To nonflower (ψ^{FN})	0.54	0.54	0.60	0.36	0.64	0.21
To flower (ψ^{FF})	0.39	0.42	0.29	0.60	0.21	0.74
Mortality	0.03	0.03	0.03	0.03	0.03	0.03

^a Notation: ψ^{ij} denotes an unconditional transition probability from stage i to stage j (T : tuber, N : nonflowering, F : flowering).

^b Relative precipitation levels held at the average and ± 1 SD of annual rainfall amount observed at Rockefeller Prairie 1991–2005.

role of information in reducing decision-improving uncertainty. In essence, this closes the loop between decisions and outcomes, because monitoring allows information from observed consequences of decisions to improve future management actions. Structural uncertainty can be reduced with the appropriate monitoring information and is relevant when we are unsure about the appropriate model for describing and making predictions about system dynamics in response to management. For this problem, we are uncertain about how burning influences the recruitment and individual growth rates of Mead's milkweed, and in turn, its rate of population growth. So, we constructed two competing models to describe alternative burn-effect hypotheses. As decisions are made into the future, our belief about which model is better evolves according to how each predicts changes in population states in response to management actions relative to observed changes. Therefore, as data are obtained following actions carried out through time, and our belief in each model is continually reassessed, tomorrow's choice of management action for a given population condition is dependent on current, cumulative evidence gathered for and against each hypothesis.

To investigate the influence of structural uncertainty on optimal decision making, we used adaptive optimization to estimate optimal policies when the most appropriate model is not known with certainty (Williams et al. 2002). Specifically, we incorporated the uncertainty about the effects of burning on Mead's milkweed population dynamics explicitly into the dynamic programming algorithm. This is simply a generalization of single-model dynamic programming to multiple models, incorporating

the current knowledge about relative model fitness into a "belief" state. The belief state, a set of probabilities attached to the models, reflects current relative confidence among the models and is tracked through time along with the population state. In an adaptive management framework, the belief state changes when new monitoring information is used to update the relative consistency of each model with the observed system. Model belief weight updating is typically performed using Bayes' Theorem (Link and Barker 2006). By folding model probabilities into the optimality equation of Bellman (1957), an optimal management policy can be computed that specifies actions according to the current state and current relative belief in the most appropriate state dynamics model (Williams et al. 2002; Moore and Conroy 2006). For this optimization, we used the same discounted and cost-weighted objective function as used for the single-model optimizations.

Because the dynamics of model uncertainty are explicitly accounted for in the optimization, the management policy can recognize population state opportunities where an action could return information useful for resolving uncertainty and, consequently, for more effective future management. Thus, our approach is an embodiment of an active adaptive approach, in which a managed system can be constructively and carefully "probed" to elicit information useful to future management.

Results

Summaries of capture history data reported in table 1 of Alexander et al. (1997) reveal that flowering, in the absence of flowering the previous year, was observed

frequently in burn years (77%) and infrequently (12% and 21%) in nonburn years. Similarly, when flowering occurred in the previous year, flowering was commonplace (93%) in burn years, but uncommon (11% and 30%) in years without burning (table 1 of Alexander et al. [1997]). In general, burning is associated with more flowering plants and more flowers per plant (Kettle et al. 2000), as well as more genotypes among smaller clones (Tecil et al. 1998; Hayworth et al. 2001). Additionally, above-average rainfall in previous years may increase the probability of transitioning to the flowering stage in the current year (Kettle et al. 2000).

Our estimated transition probabilities (Table 2; Figure 3) are generally consistent with these observed patterns. The probability of transitioning from the nonflowering stage to the flowering stage is greater if a spring burn intercedes than if not, unless prior-year precipitation has been scarce. Remaining in the flowering stage is always more likely when burning is applied than when not, except when prior year rainfall has been low, in which case the probability of remaining is about the same whether or not burned.

Adult plants will occasionally recess to tubers after flowering; the only published estimate of flowering adults reverting to root stock between years was a 12.5% rate observed by Betz (1989). Our model suggests a relatively low rate of recession to the below-ground stage from the flowering stage (1–12%; Table 2; Figure 3), but the recession rate from the nonflowering stage is appreciably greater (1–40%) and depends on management treatment and prior year rainfall. In a relatively dry prior year, our model suggests a greater tendency for nonflowering patches to transition to the dormant below-ground stage if burning is applied than if not, but when prior year rainfall is abundant, the tendency for dormancy is greatest when burning is absent.

The optimization of Model 0 (baseline) yielded a decision policy where burning was recommended in 432 (69%) of the 625 discrete population states (Figure 4A). At higher levels of any population stage (juveniles, tubers, nonflowering patches, flowering patches), rest becomes the optimal action, reflecting the incorporation of management cost in the objective function (the lack of burn in the $\{J = 0, T = 0, N = 0, F = 0\}$ population state is an artifact, because this is the state of total extirpation, for which no burning is trivially optimal).

Under the alternative structure of Model 1 (burn-enhanced), burning is optimal for fewer population states (342, or 55%) than under Model 0 (Figure 4E). Under Model 1, compared to Model 0, burning has enhanced effect for some juvenile-stage model parameters, and rest is not quite so detrimental. Because of the greater efficiency of burning under this model, and because cost remains a consideration, burning is called for under fewer circumstances as compared to Model 0.

The active adaptive decision policy for Mead's milkweed reveals an intuitive pattern for optimal management under uncertainty between models (Figure 4A–E). Policies are referenced in terms of degree of confidence in Model 1. Thus, confidence levels of 25%, 50%, and 75%

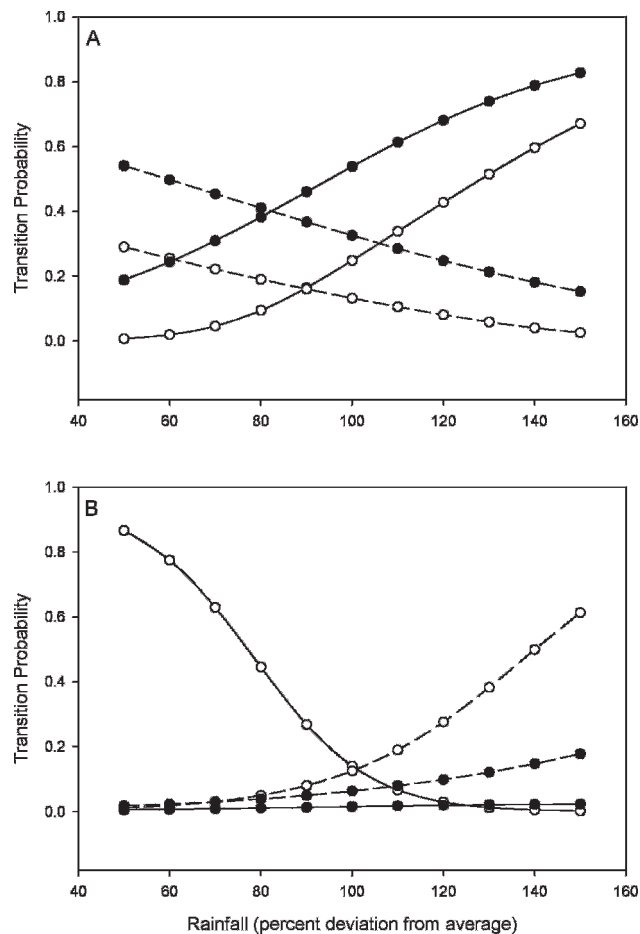


Figure 3. Estimated unconditional probabilities of transition among stages of Mead's milkweed *Asclepias meadii* based on analysis of marked individuals followed 1992–2006 at Rockefeller Prairie, Kansas. Transition probabilities are dependent on prior-year rainfall and whether dormant-season burning has (solid line) or has not (broken line) occurred. Panels reflect transitions into the flowering stage (A) and the tuber stage (B) from a previous flowering stage (●) or a previous nonflowering stage (○).

in Model 1 (Figure 4B–D) correspond to confidence levels of 75%, 50%, and 25% in Model 0, respectively. When confidence in Model 1 begins to waver from 100% (Figure 4E) to 75% (Figure 4D) confidence, the number of population conditions for which burning is optimal jumps to 393, or 63% of population states. The added burning actions have a dual purpose: they “bet-hedge” against the possibility that Model 0 is the more appropriate model for the system (thus, requiring burning at more population states), and they probe the system at relatively secure population conditions to obtain information useful to distinguish the models. This latter role exemplifies the active adaptive nature of the decision policy.

Discussion

We have demonstrated the development of a decision support application for the management of a threatened plant species about which key demographic parameters

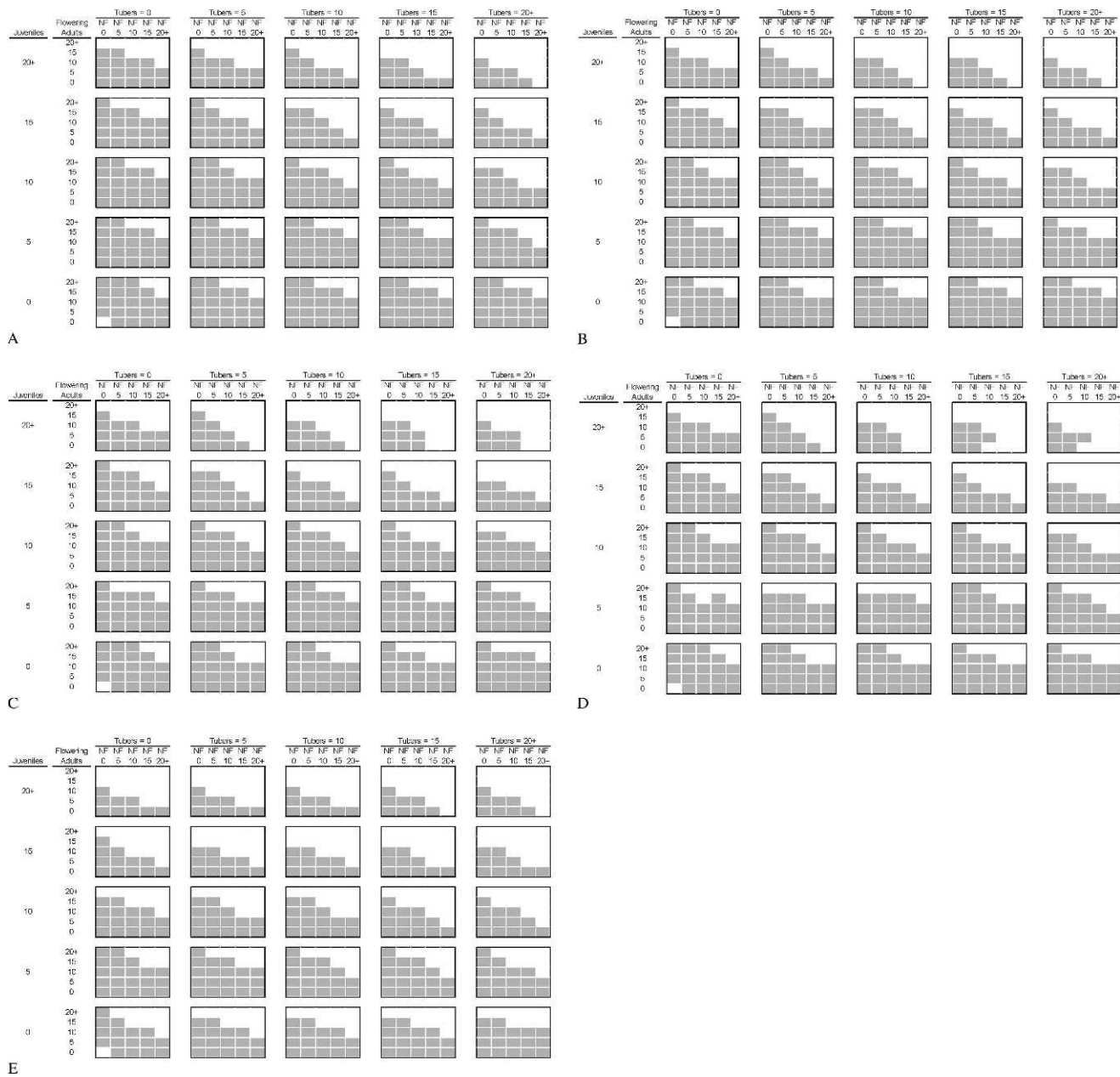


Figure 4. Optimal Mead’s milkweed *Asclepias meadii* burn-management policies for increasing levels of belief in Model 1 (“burn-enhanced” model). Shaded cells indicate burning as the optimal state-specific action, while unshaded cells indicate no burn. NF indicates “nonflowering.” Figure panels correspond to belief in Model 1 at levels of 0% (A; 100% belief in “baseline” Model 0), 25% (B; 75% belief in Model 0), 50% (C; 50% belief in Model 0), 75% (D; 25% belief in Model 0), and 100% (E; 0% belief in Model 0), respectively.

are uncertain. We synthesized current knowledge of Mead’s milkweed into a model of system dynamics that projects a population structure forward through time in response to a stochastic environmental driver (rainfall) and a management variable (burning). By using the model in conjunction with a statement of management objectives, we developed an optimal population-state-dependent decision policy that strikes a balance between population persistence and cost of actions. We posed a key uncertainty regarding dynamics of the juvenile segment as a pair of competing models, and we developed an active adaptive policy that indicates

optimal actions under combinations of current population state and current relative belief in the models. The policy explicitly recognizes the value of learning through informative actions, but only to the extent that they contribute to better performance on the management objective (Runge 2011). We see this work as an example of a successful integration of science and management through which TES recovery efforts may be most effective.

While the expression of the objective for the management of TES is usually straightforward—generally related to the future persistence and recovery of the

species—the most appropriate technical representation of the objective is not always obvious. Because we explicitly took into account the time frame for decision making, we believed that a reasonable conservation focus could be achieved through maximizing the abundance of flowering patches over an indeterminate time frame. The objective statement recognizes that the path to maximizing future abundance of flowering patches will avoid actions that would lead to extirpation in the intervening years. However, burning is always a beneficial action under these models; therefore, the cost of management should also be recognized to otherwise prevent burning as the recommended action at every population condition. We achieved this by applying a penalty to the count of flowering patches gained whenever burning is used. The penalty creates a tension between increasing number of flowering patches and spending limited resources to do so.

It is important to note that the scope of our work was the viability of Mead's milkweed exclusively. Hence, though burning (or not burning) in any given year might well be optimal for the target species, this model makes no recommendation concerning the optimal decision for managing the prairie community as a whole. As such, these results should not be interpreted as a strategy for general prairie management. In all likelihood, some fashion of mixed management scheme (spatial and temporal variation in application of treatments) will be optimal when a community-based metric is used as an optimization objective, because many prairie plants and animals would decline under a frequency of burning that is beneficial to Mead's milkweed. In addition, even within a milkweed-centric optimization criterion, there may be considerations about management history and consequent energy limitations that would restrict enhanced reproduction if burning were carried out very frequently (e.g., costs of reproduction [Obeso 2002]). For example, research on another milkweed species has revealed that pod production in one year is associated with smaller plant size and reduced flower production in the subsequent year (Chaplin and Walker 1982). Thus, any operational adaptive management strategy would likely consider more realistic objectives and models than those which we have outlined herein.

Considerations for implementing adaptive management for rare plant species

We have demonstrated the technical feasibility of developing decision guidance for a rare plant under structural uncertainty, but effective implementation of adaptive management for Mead's milkweed and other rare plant species faces certain challenges. The first is related to the distribution of Mead's milkweed across multiple ownerships that are disconnected in governance, that differ in management objectives, and that have different management tools available to them. Private lands host the largest proportion of Mead's milkweed, yet the plants occurring there are afforded no protection under the provisions of the Endangered Species Act. Though there are numerous landowner incentive programs to encourage conservation of federally listed

species, there is no single authority for prescribing optimal conservation actions. A reasonable way forward is to link management efforts across a network of conservation-focused lands where objectives, management alternatives, and monitoring systems can be aligned and coordinated, similar to the model of adaptive management employed by the National Wildlife Refuge System of the USFWS (Moore et al. 2011).

The second challenge relates to the inherent difficulty in monitoring Mead's milkweed and perhaps many other plant species. The lynchpin of any adaptive management effort is the ability to reduce uncertainty and improve management over time via feedback from monitoring system responses to past actions. However, Mead's milkweed populations are only partially observable. Juvenile and below-ground stages are effectively unobservable due to their diminutive size or subterranean condition, making them unavailable for monitoring without employing very invasive and impractical field methods; thus, half of the life-history stages used in the population model are entirely hidden. Furthermore, lacking fine-scaled monitoring, herbivory of adult stems cannot be distinguished from dormancy. The processes that lead to each of these possible outcomes may be quite different, but our models could not fully capture this dynamic. Correct identification of adult stems outside the main flowering period can be extremely difficult due to the plant's rarity, thick vegetation (especially on unburned prairies), and the specialized training that is required to distinguish nonflowering plants from similar vegetation. In practice, state-specific decisions, such as those provided by our optimization results, can only be made with respect to observable stages. Our framework presumes that the response by all four stage components can be measured and subsequently used to update credibility of each model. However, we do not take into account the reality that decisions (and hence, learning) can only be carried out with respect to the adult stages, and that this may lead to suboptimal policies.

The problem of partial observability may necessitate a modeling approach in which the selection of management actions and the updating of system knowledge is based solely on observable portions of the system (i.e., numbers of flowering and nonflowering adult patches and the number of pods per flowering patch) that serve as "proxies" for the unobservable portions. For example, transitions among the observable stages could be expressed in very simple "phenomenological" models that subsume mechanistic, biological system dynamics in a few statistically estimable transitions. Alternatively, it may be possible to model the population by treating the unobservable stages as latent system states, using Bayesian and/or state-space modeling approaches to estimate what is unseen (e.g., Buckland et al. 2004; Clark et al. 2005). Either approach constitutes a loss of system resolution, because important life stages must be inferred from the observable components, but the trade-off in management performance for the gain of less intensive monitoring may be an acceptable compromise. Furthermore, either approach would benefit by conducting small-scale, experimental plantings where

one knows exactly where the plant was placed and its age (sensu Bowles et al. 2001; Bell et al. 2003). By conducting the plantings in conjunction with some of the managed populations, it may be possible to learn more about unobservable life stages and treatment effects than would be possible in a general prairie monitoring scheme.

A technical challenge was the inability of the available optimization software to adequately address the important sources of uncertainty in the derivation of the decision policies. The software we used was able to accommodate only a few state variables and stochastic variables. Importantly, it could not accommodate partial observability, so we were unable to evaluate the effect of not being able to easily monitor juvenile and below-ground stages. As a result, our policies only incorporate a fraction of the system and observational uncertainty that currently accompanies Mead's milkweed population management. Alternative optimization techniques based on artificial intelligence, such as reinforcement learning (Sutton and Barto 1998; Fonnesebeck 2005), are able to accommodate more complex dynamics, model partial observability, and account for more sources of stochasticity. Although the solutions they provide are approximate, they may nevertheless be useful for employing more realistic models of adaptive management for Mead's milkweed and other rare plants.

Conclusions

Mead's milkweed would seem an ideal candidate for an adaptive approach to conservation decision making. There are several sources of system uncertainty and environmental stochasticity, each of which impairs the ability of managers to effectively conserve the species. Several important aspects of the plant's life history are not well-known. Yet, as we have shown, it is possible to assemble what information exists from a variety of sources with varying degrees of empirical support into a coherent model of system dynamics. Further, this model can be broadened and customized to make predictions about the species' response to management actions under a variety of assumptions about biological mechanisms.

Conservation of other rare plant species could be based on a similar approach and collection of techniques. Implementing adaptive management for rare plant conservation is not without its challenges, but we believe that they can be met. Perhaps the clearest way forward is through the establishment of a network of conservation partners that spans the public and private sectors. Here, elements of the decision problem (i.e., objectives, management alternatives, monitoring plan) can be mutually determined. A partnership will be especially advantageous in supporting the specialized monitoring that may be required, in developing the necessary models to accommodate issues in partial observability, and in conducting targeted experimentation to fold into the decision framework. Replication of decision making across multiple sites in a network is a means to more rapidly acquire understanding and improve overall conservation outcomes (Moore et al. 2011).

The understanding gained through a conservation network could ultimately be focused to the management of private lands. For example, landowners could be provided incentives for habitat management favorable for Mead's milkweed specifically and prairie ecosystems generally. Models and decision frameworks such as ours could be adapted to help conservation managers select good candidates for program enrollment from applications received (e.g., Howell et al. 2009).

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Reference S1. Morgan SW. 1980. Status report on *Asclepias meadii* Torr. Jefferson City, Missouri: Missouri Department of Conservation.

Found at DOI: <http://dx.doi.org/10.3996/012011-JFWM-007.S1> (812 KB PDF).

Reference S2. Kurz DR, Bowles ML. 1981. Report on the status of Illinois vascular plants potentially endangered or threatened in the United States. Report to the Natural Land Institute, Rockford, Illinois.

Found at DOI: <http://dx.doi.org/10.3996/012011-JFWM-007.S2> (481 KB PDF).

Reference S3. Bowles ML, McBride JL, Betz RF. 1995. Mead's milkweed (*Asclepias meadii*) restoration in Illinois and Indiana. Report to the U.S. Fish and Wildlife Service and U.S. Forest Service, Barrington, Illinois.

Found at DOI: <http://dx.doi.org/10.3996/012011-JFWM-007.S3> (1,327 KB PDF).

Reference S4. Eulinger K, Skinner M. 2005. A summary report on the status of three listed plants in SW Missouri. Report of Missouri Department of Conservation to U.S. Fish and Wildlife Service, Springfield, Missouri. Section 6 Grant E-1-43K.

Found at DOI: <http://dx.doi.org/10.3996/012011-JFWM-007.S4> (19 KB PDF).

Text S1. Methods and results of fitting multistate mark-recapture models to 252 capture histories of Mead's milkweed *Asclepias meadii* observed at Rockefeller Prairie, Kansas, 1992–2006.

Found at DOI: <http://dx.doi.org/10.3996/012011-JFWM-007.S5> (44 KB DOC).

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References

- Alexander HM, Slade NA, Kettle WD. 1997. Application of mark-recapture models to estimation of the population size of plants. *Ecology* 78:1230–1237.
- Alexander HM, Slade NA, Kettle WD, Pittman GL, Reed AW. 2009. Detection, survival rates and dynamics of a cryptic plant, *Asclepias meadii*: applications of mark-recapture models to long-term monitoring studies. *Journal of Ecology* 97:267–276.
- Bell T, Bowles M. 2006. Low fecundity and slow seedling growth in Mead's milkweed: limits to population growth and ability to produce demographic models. Abstract presented at symposium: "Ecology, evolution, and conservation of a rare prairie plant: Mead's milkweed (*Asclepias meadii*)". Lawrence: University of Kansas, 27–28 November 2006. Available: <http://www.ksr.ku.edu/Mmilkweed/> (September 2011).
- Bell TJ, Bowles ML, McEachern AK. 2003. Projecting the success of plant population restoration with viability analysis. Pages 313–348 in Brigham CA, Schwartz MW, editors. Population viability in plants: conservation, management, and modeling of rare plants. Berlin: Springer-Verlag.
- Bellman RE. 1957. Dynamic programming. Princeton, New Jersey: Princeton University Press.
- Betz RF. 1989. Ecology of Mead's milkweed (*Asclepias meadii* Torrey). Pages 187–191 in Bragg TB, Stubbendieck J, editors. Proceedings of the Eleventh North American Prairie Conference. Lincoln: University of Nebraska.
- Betz RF, Lamp HF. 1992. Flower, pod, and seed production in eighteen species of milkweeds (*Asclepias*). Pages 25–30 in Smith DD, Jacobs CA, editors. Proceedings of the Twelfth North American Prairie Conference. Cedar Falls: University of Iowa.
- Betz RF, Struven RD, Wall JE, Heitler FB. 1994. Insect pollinators of 12 milkweed (*Asclepias*) species. Pages 45–60 in Wickett RG, Lewis PD, Woodliffe A, Pratt P, editors. Proceedings of the Thirteenth North American Prairie Conference. Windsor, Ontario: Canada Department of Parks and Recreation.
- Bowles ML, McBride J, Bell T. 2001. Restoration of the federally threatened Mead's milkweed (*Asclepias meadii*). *Ecological Restoration* 19:235–241.
- Bowles ML, McBride JL, Betz RF. 1995. Mead's milkweed (*Asclepias meadii*) restoration in Illinois and Indiana. Report to the U.S. Fish and Wildlife Service and U.S. Forest Service, Barrington, Illinois (see *Supplemental Material*, Reference S3; <http://dx.doi.org/10.3996/012011-JFWM-007.S3>).
- Bowles ML, McBride JL, Betz RF. 1998. Management and restoration ecology of the federal threatened Mead's milkweed, *Asclepias meadii* (Asclepiadaceae). *Annals of the Missouri Botanical Garden* 85:110–125.
- Broyles SB, Wyatt R. 1993. The consequences of self-pollination in *Asclepias exaltata*, a self-incompatible milkweed. *American Journal of Botany* 80:41–44.
- Buckland ST, Newman KB, Thomas L, Koesters NB. 2004. State-space models for the dynamics of wild animal populations. *Ecological Modelling* 171:157–175.
- Caswell H. 2001. Matrix population models. 2nd edition. Sunderland, Massachusetts: Sinauer.
- Chaplin SJ, Walker JL. 1982. Energetic constraints and adaptive significance of the floral display of a forest milkweed. *Ecology* 63:1857–1870.
- Clark CW, Mangel M. 2000. Dynamic state variable models in ecology: methods and applications. New York: Oxford University Press.
- Clark JS, Ferraz G, Oguge N, Hays H, DiCostanzo J. 2005. Hierarchical Bayes for structured, variable populations: from recapture data to life-history prediction. *Ecology* 86:2232–2244.
- Eulinger K, Skinner M. 2005. A summary report on the status of three listed plants in SW Missouri. Report of Missouri Department of Conservation to U.S. Fish and Wildlife Service, Springfield, Missouri. Section 6 Grant E-1-43K (see *Supplemental Material*, Reference S4; <http://dx.doi.org/10.3996/012011-JFWM-007.S4>).
- Fiedler PL. 1987. Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). *Journal of Ecology* 75:977–995.
- Fonnesbeck CJ. 2005. Solving dynamic wildlife resource optimization problems using reinforcement learning. *Natural Resource Modeling* 18:1–40.
- Freeman CC. 2006. Introduction to Mead's milkweed (*Asclepias meadii* Torr.) and its habitat. Abstract presented at symposium: "Ecology, evolution, and conservation of a rare prairie plant: Mead's milkweed (*Asclepias meadii*)" Lawrence: University of Kansas, 27–28 November 2006. Available: <http://www.ksr.ku.edu/Mmilkweed/> (September 2011).
- Grman EL, Alexander HM. 2005. Factors limiting fruit production in *Asclepias meadii* in northeastern Kansas. *American Midland Naturalist* 153:245–256.
- Hayworth DA, Bowles ML, Schaal BA, Shingleton KE. 2001. Clonal population structure of the federal threatened Mead's milkweed, as determined by RAPD analysis, and its conservation implications. Pages 182–190 in Bernstein N, Ostrander LJ, editors. Proceedings of the Seventeenth North American Prairie Conference: seeds for the future, roots of the past. Mason City: North Iowa Area Community College.
- Howell JE, Moore CT, Conroy MJ, Hamrick RG, Cooper RJ, Thackston RE, Carroll JP. 2009. Conservation of northern bobwhite on private lands in Georgia, USA under uncertainty about landscape-level habitat effects. *Landscape Ecology* 24:405–418.



- Hulbert LC. 1988. Causes of fire effects in tallgrass prairie. *Ecology* 69:46–58.
- Kahn AP, Morse DH. 1991. Pollinium germination and putative ovule penetration in self- and cross-pollinated common milkweed *Asclepias syriaca*. *American Midland Naturalist* 126:61–67.
- Kephart SR. 1981. Breeding systems in *Asclepias incarnata* L., *A. syriaca* L., and *A. verticillata* L. *American Journal of Botany* 68:226–232.
- Kettle WD, Alexander HM, Pittman GL. 2000. An 11-year ecological study of a rare prairie perennial (*Asclepias meadii*): implications for monitoring and management. *American Midland Naturalist* 144:66–77.
- Kurz DR, Bowles ML. 1981. Report on the status of Illinois vascular plants potentially endangered or threatened in the United States. Report to the Natural Land Institute, Rockford, Illinois (see *Supplemental Material*, Reference S2; <http://dx.doi.org/10.3996/012011-JFWM-007.S2>).
- Link WA, Barker RJ. 2006. Model weights and the foundations of multimodel inference. *Ecology* 87:2626–2635.
- Lubow BC. 1995. SDP: generalized software for solving stochastic dynamic optimization problems. *Wildlife Society Bulletin* 23:738–742.
- Lubow BC. 1997. Adaptive stochastic dynamic programming (ASDP): supplement to SDP user's guide, version 2.0. Fort Collins: Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University.
- Menges ES. 2000. Applications of population viability analyses in plant conservation. *Ecological Bulletins* 48:73–84.
- Moore CT, Conroy MJ. 2006. Optimal regeneration planning for old growth forest: addressing scientific uncertainty in endangered species recovery through adaptive management. *Forest Science* 52:155–172.
- Moore CT, Converse SJ, Folk MJ, Runge MC, Nesbitt SA. 2010. Evaluating release alternatives for a long-lived bird species under uncertainty about long-term demographic rates. *Journal of Ornithology*. Available (Online First): <http://dx.doi.org/10.1007/s10336-010-0592-y> (October 2011).
- Moore CT, Kendall WL. 2004. Costs of detection bias in index-based population monitoring. *Animal Biodiversity and Conservation* 27(1):287–296.
- Moore CT, Lonsdorf EV, Knutson MG, Laskowski HP, Lor SK. 2011. Adaptive management in the U.S. National Wildlife Refuge System: science-management partnerships for conservation delivery. *Journal of Environmental Management* 92:1395–1402.
- Morgan SW. 1980. Status report on *Asclepias meadii* Torr. Jefferson City, Missouri: Missouri Department of Conservation (see *Supplemental Material*, Reference S1; <http://dx.doi.org/10.3996/012011-JFWM-007.S1>).
- Morris WF, Doak DF. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sunderland, Massachusetts: Sinauer.
- Nicolson CR, Starfield AM, Kofinas GP, Kruse JA. 2002. Ten heuristics for interdisciplinary modeling projects. *Ecosystems* 5:376–384.
- Obeso JR. 2002. The costs of reproduction in plants. *New Phytologist* 155:321–348.
- Pascual MA, Kareiva P, Hilborn R. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology* 11:966–976.
- Row JM, Wynia RL, Conway TC, Kindscher K. 1999. Propagation of Mead's milkweed. Pages 235–242 in Springer JT, editor. *Proceedings of the Sixteenth North American Prairie Conference*. Kearney: University of Nebraska.
- Runge MC. 2011. An introduction to adaptive management for threatened and endangered species. *Journal of Fish and Wildlife Management* 2(2):220–233.
- Sage TL, Williams EG. 1991. Self-incompatibility in *Asclepias*. *Plant Cell Incompatibility Newsletter* 23:55–57.
- Shannon TR, Wyatt R. 1986. Pollen germinability of *Asclepias exaltata*: effects of flower age, drying time, and pollen source. *Systematic Botany* 11:322–325.
- Sutton RS, Barto AG. 1998. Reinforcement learning: an introduction. Cambridge, Massachusetts: MIT Press.
- Tecic DL, McBride JL, Bowles ML, Nickrent DL. 1998. Genetic variability in the federal threatened Mead's milkweed, *Asclepias meadii* Torrey (Asclepiadaceae), as determined by allozyme electrophoresis. *Annals of the Missouri Botanical Garden* 85:97–109.
- [USDA] U.S. Department of Agriculture. 2008. PLANTS database. Available: <http://www.plants.usda.gov> (September 2011).
- [USFWS] U.S. Fish and Wildlife Service. 1988. Endangered and threatened wildlife and plants; determination of threatened status for *Asclepias meadii* (Mead's milkweed). *Federal Register* 53:33992–33995.
- [USFWS] U.S. Fish and Wildlife Service. 2003. Mead's milkweed (*Asclepias meadii*) recovery plan. Fort Snelling, Minnesota: U.S. Fish and Wildlife Service. Available: <http://www.fws.gov/midwest/Chicago/milkweedspotlight.htm> (September 2011).
- Walters CJ. 1986. Adaptive management of renewable resources. New York: Macmillan.
- Westphal MI, Pickett M, Getz WM, Possingham HP. 2003. The use of stochastic dynamic programming in optimal landscape reconstruction for metapopulations. *Ecological Applications* 13:543–555.
- White GC, Burnham KP. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(Suppl):120–139.
- Williams BK. 1989. Review of dynamic optimization methods in renewable natural resource management. *Natural Resource Modeling* 3:137–216.
- Williams BK, Nichols JD, Conroy MJ. 2002. Analysis and management of animal populations. San Diego, California: Academic Press.
- Williams BK, Szaro RC, Shapiro CD. 2009. Adaptive management: the U.S. Department of the Interior technical guide. Washington, D.C.: Adaptive Management Working Group, U.S. Department of the Interior. Available: <http://www.doi.gov/initiatives/AdaptiveManagement/index.html> (September 2011).